Seasonal Patterns and Controlling Factors of Primary Production in Puget Sound's Central Basin and Possession Sound

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Abstract
Primary production was measured using the carbon-14 uptake method to assess production and nutrient dynamics in the Central Basin and Possession Sound regions of Puget Sound. Ambient and nutrient-spiked production rates for the entire euphotic zone were determined every 2 to 6 weeks at 4 stations from October 1998 through December 2000 (n=32). Nutrient (dissolved nitrogen and phosphate) concentrations, chlorophyll *a*, incident radiation, temperature, and salinity were also measured to examine factors affecting production rates. Seasonal variation in production is well defined for all 4 stations, with summertime (May through August) levels as high as 10,000 mg C m^{-2} d^{-1}, which drop to wintertime lows usually less than 100 mg C m^{-2} d^{-1}. Like many temperate systems, a summertime low in production was also seen in June through July at all stations. Similar variation in biomass, as measured by chlorophyll *a*, was also seen. A maximal primary productivity rate was not consistently found at any particular station. Increased primary production due to the addition of a nutrient spike was seen at times at all stations during spring and, more often, summer months. Nutrient enhancement of productivity was most pronounced in Possession Sound. Nutrient stimulation was not seen at any station during the winter, when light appears to be the primary determinant of production levels. Consideration of these results along with physical data and modeling will be required to assess regional sensitivity of this part of Puget Sound to nutrient addition.

Introduction
Human population and land development have dramatically increased in the western Washington area during recent years, presumably leading to additional nutrient input into Puget Sound from both point and nonpoint sources. This stimulates the need to assess impacts of potential eutrophication in Puget Sound. Eutrophication, or adding nutrients to a basin, can result in excessive phytoplankton growth if—and only if—nutrients are limiting phytoplankton growth. Substantial increases in phytoplankton, in turn, can result in undesirable water quality impacts, such as reduced oxygen concentrations at depth, reduction in water clarity, and possible phytoplankton species shifts.

Historically, Puget Sound has not been viewed as susceptible to eutrophication because of the typically high concentrations of nutrients incoming from the Pacific Ocean, as well as strong mixing in the Main Basin of Puget Sound, which limits exposure of phytoplankton to light and therefore reduces growth. These characteristics of Puget Sound were responsible for the success of the diversion of sewage from Lake Washington to West Point (Puget Sound) in the late 1950's (Edmondson, 1991). While nutrient loading to Lake Washington caused excessive algal growth, the same loading at West Point did not. Much of the current understanding of Puget Sound phytoplankton dynamics has been based on modeling and measurements of ambient productivity and nutrients at West Point (Winter and others 1975). However, a much more complex picture is emerging, as a diversity of responses to nutrient addition is apparent both spatially and temporally within greater Puget Sound.

In the early 1980s, Harrison and others (1983) evaluated the issue of eutrophication in the Juan de Fuca Strait, Strait of Georgia, and Puget Sound. They judged potential impacts from eutrophication of the Main

Basin of Puget Sound to be relatively low. However, they reported that the more poorly flushed bays and inlets of Puget Sound, particularly in the southern ends showed depleted surface nitrate concentrations and very low oxygen concentrations at depth. They assessed that the "early warning signs of eutrophication" were already evident in these poorly flushed bays and inlets of southern Puget Sound.

The National Oceanographic and Atmospheric Administration conducted a National Assessment of Estuarine Eutrophication in the 1990s. Based on environmental attributes and human growth indicators, only a few places within Puget Sound were judged to be currently exhibiting signs of eutrophication; however, numerous places, particularly in South Puget Sound, Hood Canal, and Whidbey basins, were assessed to be highly susceptible to future deterioration from eutrophication (Bricker and others 1999).

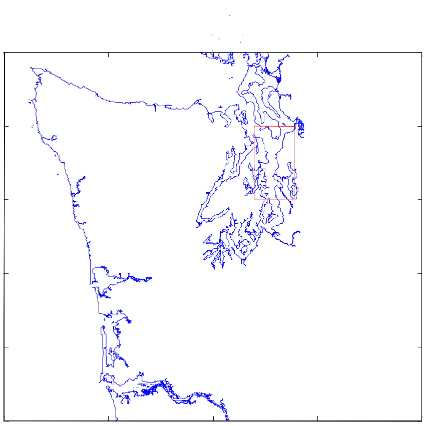
Recent studies utilizing nutrient-addition experiments on phytoplankton productivity support these conclusions, as data from Budd Inlet (Newton and others 1998a) and Hood Canal (Newton and others 1995) show substantially increased rates of primary production upon nutrient addition. Similar studies on primary production and nutrient sensitivity for the Puget Sound Main Basin and nearby Possession Sound are lacking.

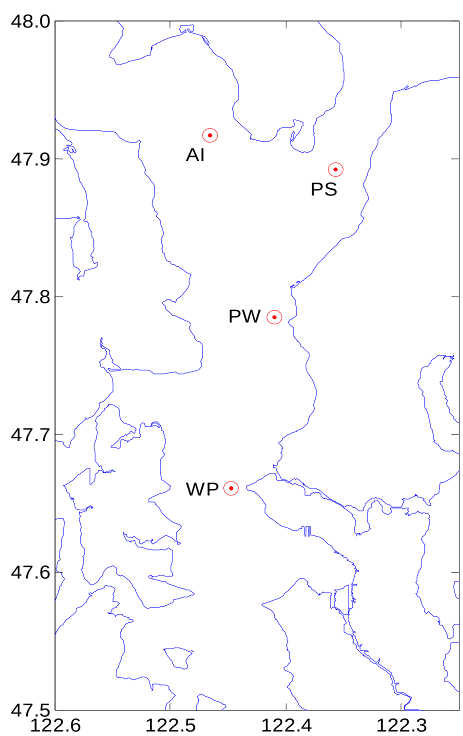
Since October 1998, the Washington State Department of Ecology and King County Department of Natural Resources have conducted a study to evaluate primary production and nutrient dynamics in Puget Sound's central basin and Possession Sound. Presented herein are preliminary results of the initial 26 months of data collection.

Methods

Four stations, located in the central basin of Puget Sound and entrances to Admiralty Inlet and Possession Sound (Figure 1), were sampled every 2 to 6 weeks (higher frequency during summer) from October 1998 through December 2000. At each station, we measured primary production (via C-14 uptake), chlorophyll *a* (extracted and *in situ* fluorescence), dissolved nutrients (nitrate, ammonium, nitrite, phosphate, and silicate), phytoplankton species, incident radiation (PAR), temperature, and salinity. Water samples were taken from depths corresponding to the 100, 50, 25, 12, 6, and 1 % surface light intensities, as estimated by secchi depth, in order to represent the entire euphotic zone (where there is enough light for photosynthesis) at each station. Standard sampling and analytical protocols are described in Newton and others (1998a) or Newton and others (1998b).

Figure 1.
Area of study. Admiralty Inlet (AI) is located at the well-mixed entrance to the estuary. Possession Sound (PS) is a partially stratified side basin. West Point (WP) is in the central main basin of Puget Sound. Point Wells (PW) is in the region where these three water bodies intersect.





The standard C-14 uptake experimental protocol was used (Strickland and Parsons 19xx). For the experiments conducted in this study, radioactive C-14 in the form of aqueous sodium bicarbonate was added to the seawater samples, which were then incubated in closed containers for 24 hours at their respective light intensities (simulated by screens in seawater-plumbed deck incubators). During photosynthesis, inorganic carbon, including any from the radioactively labeled bicarbonate, is taken up by phytoplankton and converted to cell biomass. At the end of the incubation, the amount of C-14 that was incorporated into phytoplankton biomass was obtained by filtration of the sample and measured via liquid scintillation counting. This procedure yields a measure of ambient primary production rates at each depth sampled, which can be integrated over the euphotic zone. In addition, we simulated anthropogenic nutrient loading by adding excess nutrients (ammonium and phosphate) to a duplicate set of experimental samples to determine if there was a change in the production rate due to the increased nutrient concentrations.

Primary production (P), the phytoplankton population growth rate, is the product of the phytoplankton population biomass (B) and the specific growth rate (μ) of the individuals in that population (i.e. normalized to biomass):

$$\mathbf{P = B * \mu}$$

We measured chlorophyll *a* integrated through the euphotic zone (mg chl *a* m^{-2}) as an estimate of the water column phytoplankton biomass (B) and integrated primary production (P) via C-14 uptake (mg C m^{-2} d^{-1}). Unfortunately, because the cellular content of chlorophyll is variable, the use of chlorophyll to indicate phytoplankton biomass is an estimate. Thus, with measurements of both P and B, an approximation of specific growth rate (P:B) can be made, however this also will be biased by any variation in the cellular carbon to chlorophyll ratio.

Results and Discussion

The complete database of all data from the project is housed at both the Washington State Department of Ecology and King County Department of Natural Resources.

Scales of Variation

Spatial

During the growing season, considerable variation in phytoplankton production was found between the four stations (Figure 2a). A consistent pattern in the spatial variation of these measurements was not observed; the location of highest or lowest daily production for any given sampling date was not found consistently at any particular station.

Averaging these daily rates over the entire year, the seasonally weighted annual production was found to be highest at West Point in both 1999 and 2000 (Table 1). In 1999, production levels were approximately the same at Admiralty Inlet, Possession Sound, and Point Wells. In 2000, the lowest production was found at Possession Sound. While annual production stayed constant at Possession Sound, it increased by 35 to 43% at all other stations from 1999 to 2000. This interannual variation will be examined in more detail below.

Seasonal

Consistent with Puget Sound's temperate location, a distinct seasonal pattern in primary production was observed at all stations for both years (Figure 2a). Lower production occurred in winter months with higher levels observed between the months of April to September. This growing season was characterized by a spring bloom, followed by a distinct low in production, then subsequent summer and fall blooms. Phytoplankton biomass, as indicated by chlorophyll *a*, also showed this seasonal trend (Figure 2b). Since phytoplankton populations can change rapidly on a much shorter time scale than we measured, this view could be missing much in terms of temporal dynamics.

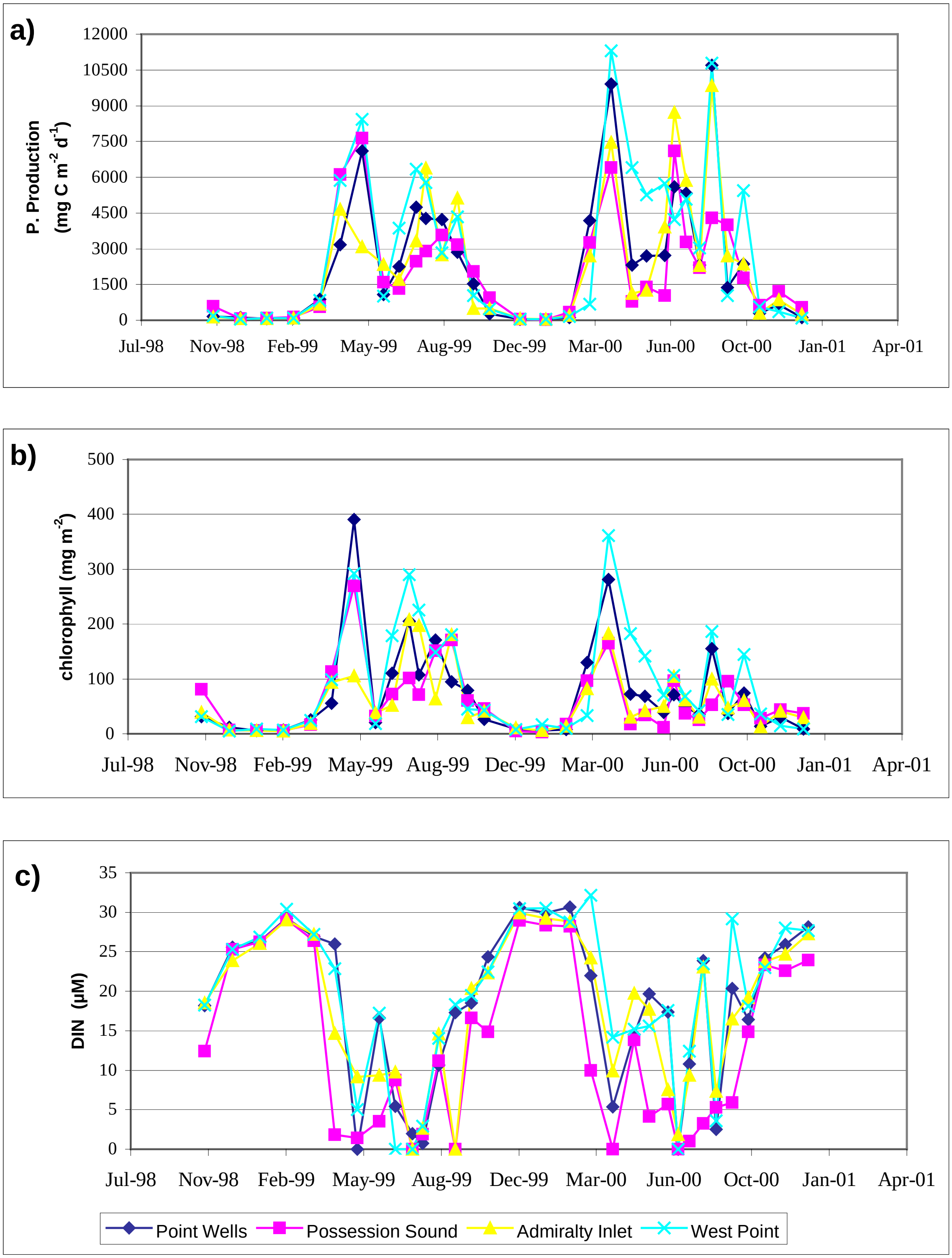


Figure 2. Seasonal pattern of (a) primary production, (b) phytoplankton biomass, as indicated by chlorophyll *a*, and (c) surface DIN for each station for two years. Production and chlorophyll values are integrated over the euphotic zone.

Table 1. Average daily production (in mg C m^{-2} d^{-1}) for each station in 1999 and 2000. Note that annual production values are not the result of a continuous data set, but are a best estimate from the 15 or so dates that were sampled per year.

	Admiralty Inlet	Possession Sound	Point Wells	West Point
1999	1886	2127	2028	2559
2000	2691	2132	2899	3462
% increase from 1999 to 2000	43	0	43	35

Interannual

Annual integrated production was higher by 35-43% during 2000 relative to 1999 at Admiralty Inlet, Point Wells and West Point, while there was no change at Possession Sound. To clarify the possible mechanisms driving this difference, we looked at several factors affecting phytoplankton production (Table 2). For 2000, there was a smaller population of phytoplankton, as indicated by integrated chlorophyll *a*, at all stations but particularly at Possession Sound (-36%). This observation, coupled with the increase in production during 2000 at most stations, implies substantially higher specific growth rates must have occurred during 2000, as indicated by the P:B ratio (+42-77%). However, at Possession Sound, the decrease in chlorophyll was marked enough to result in no corresponding increase in production. Possession Sound was also unique in that surface dissolved inorganic nitrogen (DIN = nitrate + nitrite + ammonium) remained the same, rather than increasing as at the other stations.

Table 2. Annual percent increase in production and factors affecting production. Direction of change from 1999 to 2000 is indicated. Numerical shifts are listed in parentheses.

From 1999 to 2000				
	Admiralty Inlet	**Possession Sound**	**Point Wells**	**West Point**
Integrated Production (mg C m^{-2}) per year	Increased (43)	No change (0.3)	Increased (43)	Increased (35)
Solar Radiation (moles m^{-2}) per year	Increased (15)	Increased (15)	Increased (15)	Increased (15)
Surface DIN (µM) per year	Increased (19)	No change (0.4)	Increased (10)	Increased (18)
Integrated Chlorophyll (mg chl m^{-2}) per year	Decreased (-16)	Decreased (-36)	Decreased (-19)	Decreased (-5)
P:B (mg C mg chl^{-1}) per year	Increased (69)	Increased (57)	Increased (77)	Increased (42)

To understand these results, we examined these patterns in concert with certain physical factors of the greater Puget Sound system: offshore upwelling of nutrient-rich deep water (Bakun upwelling index, from NOAA; http://www.pfeg.noaa.gov/), local river input (flow data, from USGS; http://water.usgs.gov/wa/nwis/) and local winds (from NDBC; http://seaboard.ndbc.noaa.gov/)—all averaged over the entire year. From 1999 to 2000 upwelling increased 11% and river input decreased 7 and 11% for the Skagit and Snohomish Rivers, respectively. These differences are consistent with a stronger oceanic input and weaker fresh water input into Puget Sound for 2000. Winds, which cause mixing of the water column, increased 16% in 2000.

These trends in external physical forcings are compatible with the phytoplankton production and biomass results. A stronger oceanic input during 2000 suggests that more nutrient-rich deep water could have entered Puget Sound at depth through Admiralty Inlet. As this deep water is mixed to the surface, especially in the southern part of the Main Basin at The Narrows (Ebbesmeyer and Barnes 1980), nutrients would become available for photosynthesis. Consistent with known circulation patterns (Cannon and others

1984; Cannon, and others 1990; Ebbesmeyer and Cannon 2001), these nutrients might travel back through the Main Basin, where the West Point, Point Wells and Admiralty Inlet stations are located, bypassing the more river-dominated side-basin of Possession Sound. This could possibly explain the differences in nutrient availability between stations.

The stronger wind speeds during 2000 likely translated to increased mixing of the water column. This could cause nutrients to be mixed up towards the surface and phytoplankton to be mixed down below the euphotic zone, where light is not available for photosynthesis. This conceivably could produce a decrease in chlorophyll (i.e. biomass), as was measured at all stations.

Factors affecting primary production

Correlation of primary production and chlorophyll

Chlorophyll is sometimes used to approximate primary production when the latter measurements do not exist. During our study, the variation measured in production was found to be only partially correlated with observed variations in chlorophyll (Figure 3). Linear regression R^2 values ranged from 0.52 (Admiralty Inlet) to 0.77 (West Point). This moderate level of coupling between production and chlorophyll at these areas implies that the production per unit chlorophyll is not a constant, that loss processes (grazing, mixing, sinking) are active, that phytoplankton C:chl ratios vary, or a combination of these factors. We include this analysis to show that measuring chlorophyll alone is not a very precise means of determining production rates in this region.

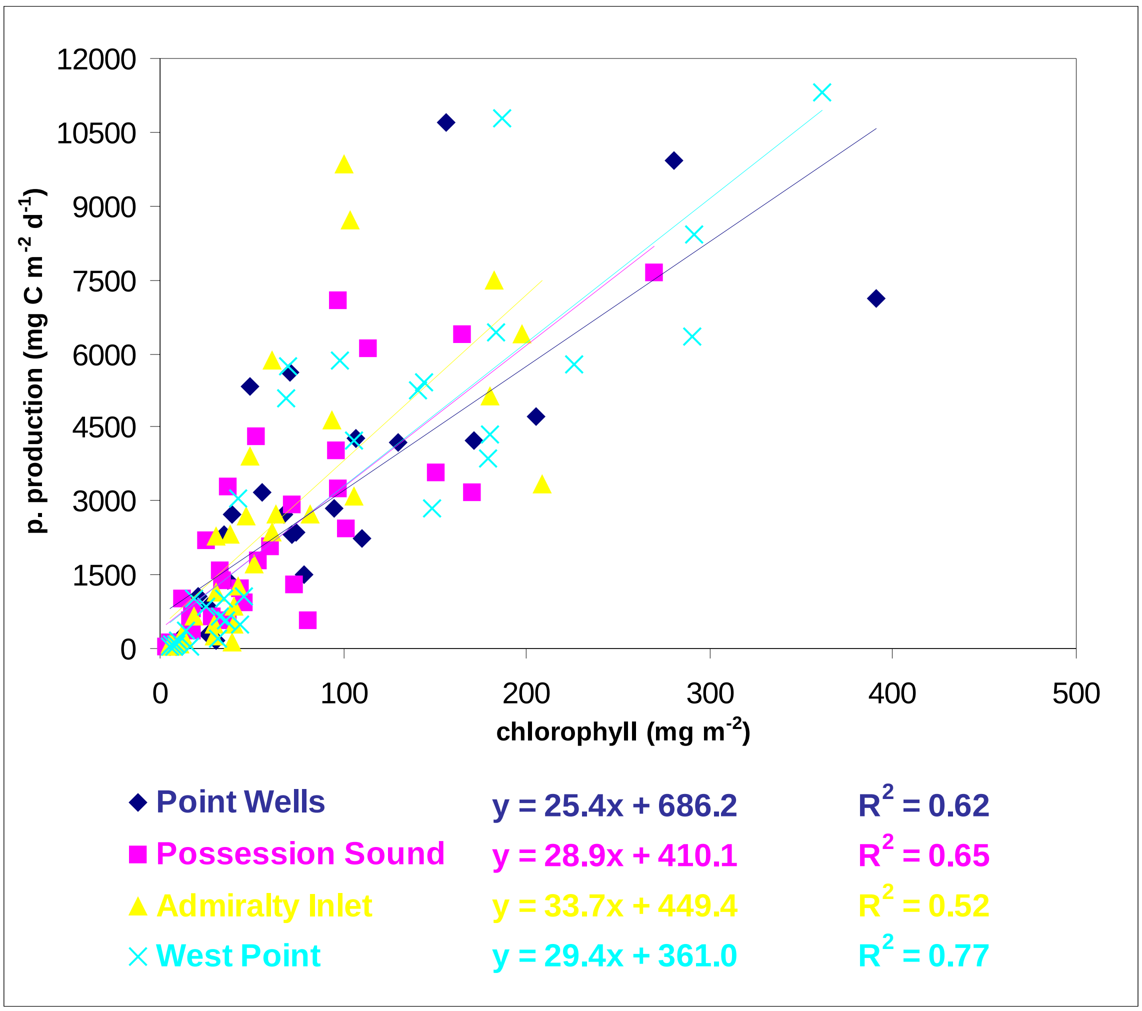


Figure 3. Correlation of primary production and phytoplankton biomass (chlorophyll *a*). Values are integrated over the euphotic zone.

Seasonal variation in factors affecting primary production
Productivity levels were typically below 100 mg C m^{-2} d^{-1} at all stations during winter months. A strong linear correlation of R^2=0.78 was found between wintertime production and irradiance (Figure 4). This strong correlation indicates that sunlight availability may be limiting primary production during winter. This relationship is not found during the spring through fall, implying that other factors are controlling production, such as nutrient availability, grazing losses, or mixing losses.

A shift from low to high primary production and phytoplankton biomass occurred in spring at all four stations (Figure 2a). P:B ratios also increased. During this time, light becomes more abundant than in winter and nutrient levels in the euphotic zone are high. The increase in production is likely due to a higher specific growth rate (μ), consistent with an abundance of light and nutrients, and also an accumulation of biomass.

By late spring, light is available but nutrient concentrations drop substantially, especially in 1999 (Figure 2c). Production rates and biomass similarly drop with a lag of approximately one month (Figure 2b). The timing of the transition from high to low nutrients and the subsequent spring phytoplankton decline was centered around May in 1999 and April in 2000. Decreased production and biomass could also result from increased zooplankton grazing and/or losses due to periodic mixing below the euphotic zone.

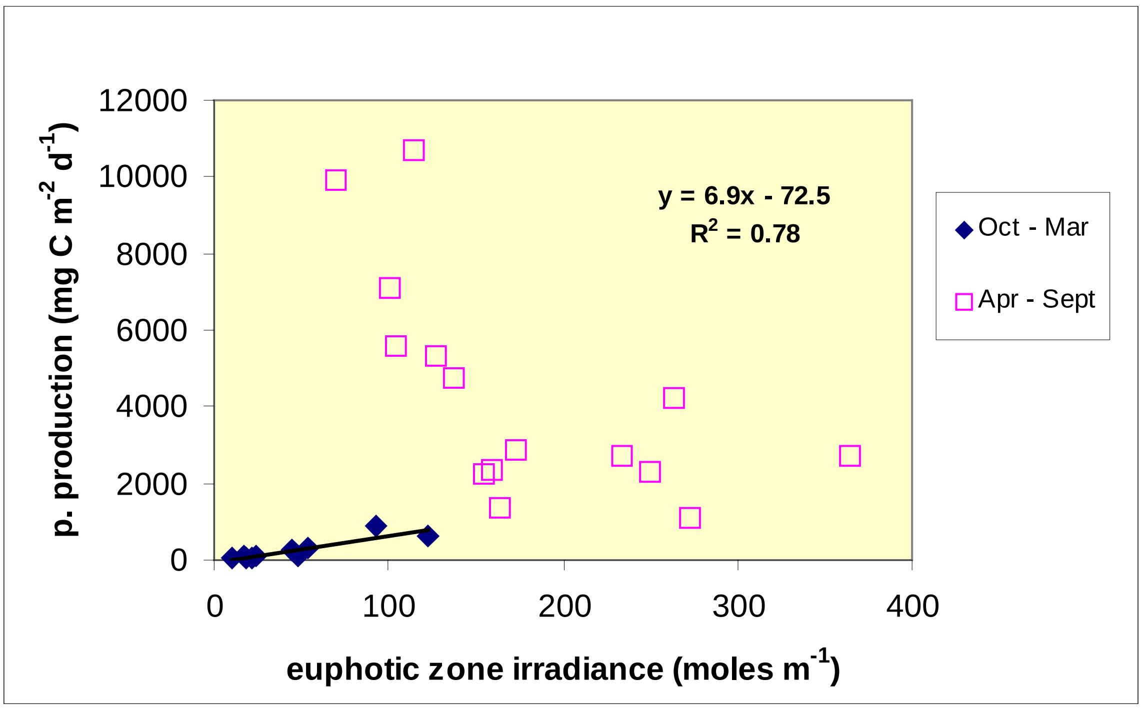


Figure 4. Correlation of integrated primary production with PAR integrated over the euphotic zone for duration of study at Point Wells. Both variables are daily measurements.

Production rates and biomass during the summer and fall months were elevated at times, indicating sporadic blooms, but usually were not as high as those seen during the spring bloom. This indicates a very dynamic environment in terms of growth conditions such as mixing, nutrient availability, and grazing pressure.

A consistent seasonal pattern in P:B ratios ($\cong\mu$) was not found. P:B values during 1999 were higher in spring relative to summer, whereas the opposite trend was observed during 2000. Values of P:B during summer 2000 were much higher (~80-110 mg C mg chl^{-1} d^{-1}) than the maximum found during 1999 (~50-

60 mg C mg chl^{-1} d^{-1}). Incident PAR was about 25% higher during summer 2000 when our observations were made and may explain some of this difference.

Controlling factors

It is strongly suggested that primary production in central Puget Sound is controlled by light availability in winter (October to March; Figure 4). However, the factors controlling primary production during the other months are more difficult to assess with the present analysis. Losses of phytoplankton biomass to grazing were not measured in this study. Losses due to mixing of cells below the euphotic zone will await further analysis with a coupled hydrodynamic-water quality model.

During the growing season, however, all stations show large increases in production as a result of added nutrients; by as much as 2 g C m^{-2} d^{-1}, implying some degree of nutrient control (Figure 5). To assess nutrient sensitivity, we established three thresholds for evaluation (Table 3). We assessed the number of times that the increase of the nutrient-spiked production was greater than 450 mg C m^{-2} d^{-1} over the ambient production. We also assessed the number of times the increase in nutrient-spiked production was 15% or more of the ambient production. Finally, we assessed the number of times that the DIN decrease over 24 hours was 5 uM more in the spiked treatment than in the ambient treatment, implying greater nutrient uptake.

Table 3. Increases in production due to nutrient addition. Number of times threshold was surpassed at each station, out of a total of 32 sampling dates. Possession Sound stands out as being the most sensitive to added nutrients.

# Episodes/32				
	Admiralty Inlet	**Possession Sound**	**Point Wells**	**West Point**
Increased Production (>450 mg C m^{-2} d^{-1})	6	**9**	6	8
Increased Production (>15%)	7	**11**	8	8
Increased Nutrient Util. (spike>ambient+5uM)	6	**12**	7	8

Episodes where these three thresholds were surpassed occurred at every station, no less than 19% (Point Wells, increased carbon by weight and Admiralty Inlet, increased carbon by weight and nutrient utilization) and up to 38% (Possession Sound, nutrient utilization) of the time (Table 3). Possession Sound appears to be consistently the most sensitive area to nutrient addition, judged by all three thresholds. However, all stations exhibited nutrient enhanced production. In winter, no significant increases in production in the nutrient added experiments were seen at any stations, as might be predicted if the system is light limited.

The increase in primary productivity due to nutrient addition ranged as high as 77% of the ambient production, on a given date. Overall annual percent increase in production due to nutrient addition was lower than that observed in Budd Inlet (Newton and others 1998a) and Hood Canal (Newton and others 1995). Slight interannual variation in the strength of the nutrient response is evident. The increase in production due to addition of nutrient spike was greater in 1999 than in 2000 (Figure 5), consistent with the pattern described previously of less nutrient availability in 1999.

Emerging Synthesis

Strong spatial and temporal variations in productivity have been observed at all four stations. We are in the process of assessing causative factors. Comparing the 1999 and 2000, data we surmise that stronger solar radiation, stronger oceanic input, and more mixing occurred in 2000. Despite this interannual variation, increased production due to nutrient addition was seen at all stations in both years. All stations show nutrient sensitivity; however, it was most pronounced in Possession Sound, which is consistent with the greater stability of this region. The next step to be taken with these data is to determine if increased carbon produced in response to added nutrients is of a magnitude that would significantly affect things such as dissolved oxygen and other trophic levels of the food web. This will require modeling of physical, chemical, and biological processes in the basin.

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